

THE STRUCTURES CALLED PARAMERES IN
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Handlirsch and other recent investigators who have figured the genitalia of male Thysanuroid Apterygotan insects, apply the term "parameres" to the processes labelled *am*, on each side of the aedeagus, labelled *ae* in Fig. 7 of the Thysanuroid insect *Machilis*. The structures labelled *am* in Fig. 7 of *Machilis*, however, are processes (sometimes interpreted as endopodites) of the coxites *cx*, or basal segments of the gonopods of the ninth abdominal segment, and thus differ from the true parameres of higher insects, in which the parameres arise as lateral derivatives of a pair of lobes borne on the ninth abdominal segment, during the development of such higher insects as the Coleoptera. On this account, the processes *am* of the coxites *cx* of such Apterygota as *Machilis* (shown in Fig. 7) may be designated as *andromeres*, to distinguish them from the true parameres of higher insects, which are described later.

Verhoeff, and other students of the Dermaptera, apply the designation "parameres" to the structures labelled *pa* in Fig. 2, which are lateral processes of the slender paired penes *pe* (borne on a common apodeme labelled *pf*) in such Dermaptera as *Anisolabis*, shown in Fig. 2. Unless the structures labelled *pa* in Fig. 2 are homologous with similarly located structures borne on each side of the paired penes of male Ephemerida, they are peculiar to the Dermaptera alone (and the Dermaptera differ from the bulk of their Orthopteroid relatives in the nature of the male genitalia). Since the structures labelled *pa* in Fig. 2 of the Dermapteron *Anisolabis* are not strictly homologous with the true parameres of higher insects, they may be called *parandrites*, to distinguish them from the true parameres, which arise as lateral derivatives of a pair of lobes borne on the ninth sternite during the development of male Coleoptera.

In such Coleoptera as the one shown in Fig. 8, a prong-like paramere, bearing the label *pm*, occurs on each side of the aedeagus, labelled *ae* in Fig. 8; and these parameres are said to arise as lateral derivatives of a pair of lobes borne on the ninth sternite in developing Coleoptera. Verhoeff and others have likewise applied the designation parameres to these structures in male Coleoptera (*i.e.*, the structures bearing the labels *pm* and *h* in Fig. 8), and it is here

suggested that the term parameres be restricted to these structures and the parts strictly homologous with them in other male insects.

The parameres of male Coleoptera are not forcipate, so that the Coleoptera are set off from the "forcipate" series of Holometabola by this feature. In fact the Coleoptera are rather isolated Holometabola which have retained more Protorthopteroid (or Dermapteroid) features than most of the other members of the Holometabolous group.

The ninth sternite, or hypandrium, *ha*, is rather normally developed in the Coleopteron shown in Fig. 8 (although the hypandrium shows some indications of becoming lateroverturned, or shifted up into the insect's left side), but in many other Coleoptera the ninth sternite becomes slender and tongue-like and the male genitalia undergo considerable shifting about.

The proctiger, or anus-bearing segmental complex labelled *pg* in Fig. 8, apparently contains the tenth segment, with which the eleventh segment and the anus-bearing nonsegmental telson have united—unless these structures have become atrophied instead of uniting with the tenth segment. Due to a slight torsion, or shifting of the parts below it, the proctiger, *pg*, appears to be somewhat displaced over toward the insect's left side in the Coleopteron shown in Fig. 8.

The claspers in the males of such Hymenoptera as the ants have long been homologized with parameres by Emery, Wheeler, and other students of the Formicidae; and other investigators have recently homologized the genital forceps of male sawflies with the parameres of male Coleoptera, but no one has apparently followed this idea to its logical conclusion and homologized the parameres of male Hymenoptera with the genital forceps of other Holometabola belonging to the "forcipate" series (*i.e.*, the Mecoptera, Trichoptera, Diptera, etc.), since the segments of the genital forceps are usually interpreted as coxites and styli of the gonopods of the ninth abdominal segment in the other members of the "forcipate" series. In the present paper, however, the forcipate claspers of the rest of the series of Holometabola are likewise homologized with the parameres of male Coleoptera, since the forceps of all of these Holometabola are homologous with the forceps of the Hymenoptera, and if the latter are really homologous with the parameres of male Coleoptera (as is claimed by all recent investigators), then the forceps should be interpreted as parameres throughout the entire series of "forcipate" Holometabola.

The parameres of a typical male sawfly, such as the one shown in Fig. 6, are composed of a basal ring, *gc* (sometimes called the

gonocardo), a shaft region, *gs* (sometimes called the gonostipes), and a distal clasper, or harpago, *h* (also called the harpe, cochliarium, etc.). In the primitive sawfly *Xyela*, shown in Fig. 6, the basal ring, *gc*, is notched and its halves are still closely associated with the bases of the shafts, *gs*, thus suggesting that the basal ring may have arisen through the union of detached basal portions of the shafts. The shafts, *gs* of Fig. 6, or *hg* of Fig. 3, are secondarily demarked into smaller areas; and the claspers, *h*, are divided into two parts in the sawfly *Xyela* shown in these figures.

The aedeagus, *ae*, is composed of two penis valves in such sawflies as *Xyela* (Fig. 6) and this suggests that the aedeagus of higher forms may have arisen from the union of paired structures of this type. The so-called sagittae and volsellae of higher Hymenoptera may represent detached portions of the shafts of the genital forceps (or they may have arisen independently in the areas near the base of the aedeagus) but the homologies of these structures, and their mode of origin throughout the order Hymenoptera, have not been definitely determined.

In the sawfly *Xyela* shown in Fig. 3 the ninth tergite, or epanthrium, *gt*, is much reduced, but the ninth sternite, or hypandrium, *gs*, is well developed, as is also the case in most male sawflies. The proctiger, or anus-bearing segmental complex, labelled *pg* in Fig. 3, apparently represents the tenth segment, with which the cercus-bearing eleventh segment and the anus-bearing telon have apparently united—unless these structures become atrophied instead of uniting with the tenth segment.

The structures labelled *c* in such sawflies as *Xyela*, shown in Fig. 3, are here interpreted as the cerci, although some recent investigators consider that they represent appendages of the tenth segment, called socii. Similar structures in female Mecoptera, however, are interpreted as cerci and it is very probable that these structures represent cerci in the Hymenoptera also.

In male Mecoptera, such as the one shown in Fig. 1, the genital forceps are composed of a basal segment, or harpagoger, *hg*, and a distal segment, or harpago, *h* (also called the harpé), forming the clasper proper. Most of the recent investigators who have figured the parts in male Mecoptera consider that the harpagoger, *hg*, and harpago, *h*, represent the coxite (or coxopodite) and stylus of the gonopods of the ninth segment and the writer likewise interpreted the parts in question as segments of the styli of the gonopods of the ninth segment, in former papers. If the genital forceps of male Hymenoptera really represent parameres, however, then the genital

forceps of male Mecoptera also represent parameres, since the structures in question are clearly homologous in both groups of insects and are so interpreted in the present paper.

The distal segments, or harpagones, of the genital forceps are reduced in such Mecoptera as *Bittacus*, in which the aedeagus becomes long and coiled, resembling in this respect the aedeagus of certain higher Diptera. The valves which occur near the base of the aedeagus in many Panorpid, have been figured elsewhere, and need not be further considered here.

The ninth tergite, or epandrium, *ea*, is well developed in the Mecopteron shown in Fig. 1, and the hypandrium, or ninth sternite, *ha*, is typically large and well developed in male Mecoptera, and frequently bears distinctive processes, etc., of value for determining the species of these insects.

The proctiger, *pg*, apparently represents the tenth segment, with which the cercus-bearing eleventh segment and anus-bearing telson have united—or they have become atrophied, if they did not unite with the tenth segment. The cerci, *c*, of Fig. 1, are reduced in male Mecoptera, although they are usually two-segmented, and are borne on a distinct eleventh segment in female Mecoptera.

In the males of certain Trichoptera, such as the one shown in Fig. 5, the genital forceps are composed of two segments, which are labelled *hg* and *h* in Fig. 5. The basal segment labelled *hg* in Fig. 5, evidently corresponds to the basal segment, or harpagoger, *hg*, of the genital forceps of the male Mecopteron shown in Fig. 1, and the distal segment, labelled *h*, in Fig. 5, evidently corresponds to the distal segment, or harpago, *h*, of the forceps of the male Mecopteron shown in Fig. 1; and if the genital forceps of the male Mecopteron shown in Fig. 1 (and the sawfly shown in Fig. 3) are parameres, then the genital forceps of the male Trichopteron shown in Fig. 5 must also be regarded as forcipate parameres.

The ninth tergite, or epandrium *ea*, is quite well developed in the male Trichopteron shown in Fig. 5, but the hypandrium, or ninth sternite, *ha*, does not project posteriorly to any extent in most Trichoptera, as it does in the male Mecoptera, sawflies, etc., shown in Figs. 1, 3, etc.

In many primitive Diptera belonging to the suborders Nematocera and Orthorrhapha Brachycera, the genital forceps of the male are composed of two segments, as is the case in the male Rhagionid (Leptid) shown in Fig. 9. The basal segment, *hg*, of the genital forceps of the Dipteron shown in Fig. 9, evidently corresponds to the basal segment, or harpagoger *hg*, of the forceps of the male

Mecopteron shown in Fig. 1, and the distal segment, *h*, of the genital forceps of the Dipteran shown in Fig. 9 evidently corresponds to the distal segment, or harpago, *h*, of the male Mecopteron shown in Fig. 1; and the genital forceps of these insects are evidently homologous with the structures interpreted as forcipate parameres in male sawflies and other Hymenoptera, although the decision as to whether the genital forceps of male Diptera, etc., represent forcipate parameres, or not, depends upon the correct identification of the genital forceps of male Hymenoptera as forcipate parameres.

Snodgrass, and other investigators who accept de Meijere's interpretation of the genital forceps of male Diptera as modified gonopods of the ninth abdominal segment, regard the basal and distal segments of the forceps as the coxites (or coxopodites) and styli of the gonopods in these insects; and the writer formerly interpreted the segments of the genital forceps as parts of the styli of the gonopods of the ninth segment and designated the basal segment of the forceps as the basistyle, and the distal segment as the dististyle, in male Diptera. In the present paper, however, the genital forceps of male Diptera (and other "forcipate" Holometabola) are interpreted as forcipate parameres simply because the evidence is inescapable that the genital forceps of these insects are homologous with the genital forceps of male sawflies and other Hymenoptera (whatever these may be), and if recent investigators are correct in identifying the genital forceps of male Hymenoptera with the parameres of male Coleoptera, there seems nothing left to do but follow this hypothesis to its logical conclusion and interpret the genital forceps of the Diptera and the rest of the "forcipate" Holometabola, also, as forcipate parameres. It must be admitted, however, that the evidence thus far produced by those who maintain that the genital forceps of male Hymenoptera represent the parameres of male Coleoptera is not entirely satisfactory, but since this view is accepted by all recent investigators, it may be used as a "working hypothesis" in attempting to homologize the parts of the genital forceps in the Holometabolous series, and for this purpose it is accepted, provisionally, in the present paper.

The ninth tergite, or epandrium, *ea*, is retained as a distinct plate in the male Rhagionid (Leptid) shown in Fig. 9, and the ninth sternite, or hypandrium, *ha*, is still distinct from the basal segments of the forceps in this rather highly specialized Dipteran, although in the males of certain Tipulidae, Mycetophilidae, and other representatives of the primitive suborder Nematocera, the basal segments of the genital forceps frequently tend to unite with the ninth sternite.

The structures labelled *c* are interpreted as the cerci in the Dipteron shown in Fig. 9, although some investigators regard these structures as socii, or appendages of the tenth segment in the Diptera. The structures in question, however, are composed of two segments in female Stratiomyidae, certain Mycetophilidae, etc., and are evidently homologous with the structures interpreted as cerci in female Mecoptera, etc., and on this account the structures in question are interpreted as cerci in the male Diptera here described.

It is extremely difficult to interpret the parts of the genitalia of male Cyclorrhaphous Diptera in terms of the parts of the genitalia of male Nematocera and Orthorrhapha Brachycera, so that the interpretations here suggested for the parts in the males of the higher Cyclorrhapha, such as *Phormia regina*, shown in Fig. 4, must be regarded as purely tentative, although these interpretations are based upon the study of an extensive series of Diptera which are not figured here and the conclusions here expressed are not based upon a direct comparison of the highly specialized *Phormia* with the rather primitive Rhagionid (Leptid) shown in Fig. 9, but are suggested by the condition found in male Syrphidae and other forms intermediate between these two widely separated types of Diptera.

The paired, so-called posterior gonapophyses, labelled *b* in Fig. 4 of *Phormia* (only one of these is shown in the lateral view of *Phormia*), are here interpreted as the distal segments, or harpagones, *h*, of the forcipate parameres of the male Rhagionid (Leptid) shown in Fig. 9, and the paired, so-called anterior gonapophyses, labelled *a* in Fig. 4 of *Phormia*, are here regarded as representing at least a part of the basal segments of the forcipate parameres, labelled *hg* in the male Rhagionid shown in Fig. 9. It is possible that a portion of the basal segment of the forcipate parameres has united with the ninth tergite, labelled *gs* in Fig. 4 of *Phormia*, but this does not alter the fact that the structures labelled *a* and *b* in *Phormia* (Fig. 4) appear to correspond, in a general way, to the basal and distal segments of the forcipate parameres bearing the labels *hg* and *h* in the Rhagionid shown in Fig. 9. The reasons for adopting this view will be presented elsewhere since it is necessary to include the figures of male Syrphidae and other intermediate forms to illustrate the stages in the transformation of the segments of the genital forceps into the anterior and posterior gonapophyses of the higher Cyclorrhapha.

The structures labelled *ss* in Fig. 4 of *Phormia* are here interpreted as appendages of the ninth tergite, called surstyli in other insects; and the structures labelled *c* in Fig. 4 of *Phormia* are here

interpreted as cerci—as is also done by other students of the Cyclorhapha, although Snodgrass considers that these structures are lateral lobes of the tenth tergite. The proctiger, *pg*, of *Phormia* probably represents the tenth segment, with which the cercus-bearing eleventh segment (and anus-bearing telson) have united, unless the latter becomes atrophied instead of uniting with the tenth segment.

The evidence for considering that the plate bearing the label 7 + 8 in Fig. 4 of *Phormia* represents the lateroverturned seventh sternite and inverted eighth sternite (instead of the eighth tergite alone) has been briefly presented in other articles dealing with this subject, but a more detailed consideration of the evidence upon which this interpretation was based can be more profitably discussed elsewhere, since it is the purpose of this preliminary paper merely to set forth the view that if the genital forceps of male Hymenoptera are actually homologous with the parameres of male Coleoptera then the genital forceps of male Diptera and other members of the "forcipate" series of Holometabolous insects must also be regarded as forcipate parameres.

ABBREVIATIONS.

a	Anterior gonapophyses, or harpagogers	ha	Hypandrium, or ninth sternite
ae	Aedeagus	hg	Harpagoger, or basal segment of forceps
am	Andromeres	pa	Parandrites
b	Posterior gonapophyses, or harpagones	pe	Paired penes
c	Cerci	pf	Penifer, or penis-bearing apodeme
cx	Coxites (coxopodites)	pm	Parameres
d	Genital spine	pp	Paraprocts
ea	Epandrium, or ninth sternite	s	Sternite (segment indicated by numeral)
gc	Gonocardo, or basal ring of forceps	ss	Surstyle
gs	Gonostipes, or shaft of forceps	st	Styli
h	Harpago or distal segment of forceps	t	Tergite (segment indicated by numeral)

EXPLANATION OF PLATE I.

FIG. 1. Lateral view of terminalia of a Mecopteron, *Taeniochorista*.

FIG. 2. Ventral view of genitalia and terminal structures of a Dermapteron, *Anisolabis maritima*.

- FIG. 3. Lateral view of terminalia of a sawfly, *Xyela* sp.
FIG. 4. Lateral view of terminalia of a Cyclorrhaphous Dipteran, *Phormia regina*.
FIG. 5. Lateral view of terminalia of a Trichopteron.
FIG. 6. Ventral view of genital forceps of *Xyela* sp.
FIG. 7. Ventral view of ninth segment and its appendages in a Thysanuroid insect, *Machilis variabilis*, redrawn from Snodgrass, 1935.
FIG. 8. Lateral view of terminalia of a Lampyroid Coleopteron.
FIG. 9. Lateral view of terminalia of a Rhagionid (Leptid) Dipteran, *Rhagio* sp.
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Collecting at Lakehurst, N. J., around Christmas, 1936.—In the past winter of 1935–36 the weather here in Lakehurst was cold from December 10 to March 10.

This winter (1936–1937) so far conditions were altogether different. On December 25 and 26 a few *Conistra* and *Graptolitha* were attracted to bait. The weather was clear and moderate. On December 27 it was cloudy and quite warm—around 62° in the day time and hardly less than 52 after dark. The result in securing specimens was remarkable. Some trees had as many as a dozen specimens, mostly *Conistra* and *Plathypena scabra* Fabr., even two *Glaea viatica* Grt. and *pastillicans* Grt., a few *Peridroma saucia* Hbn. and eleven different species of *Graptolitha*, including *lemmeri* B. & Benj. and *viridipallens* Grt. Some of the latter two species bleeding, *i.e.*, perfectly fresh when pinned. There were also several Micro-Lepidoptera, quite a few ants and some other insects at the bait.—FREDERICK LEMMER.